Recognition of other species' aerial alarm calls: speaking the same language or learning another?

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Alarm calls given by other species potentially provide a network of information about danger, but little is known about the role of acoustic similarity compared with learning in recognition of heterospecific calls. In particular, the aerial 'hawk' alarm calls of passerines provide a textbook example of signal design because many species have converged on a design that thwarts eavesdropping by hawks, and call similarity might therefore allow recognition. We measured the response of fairy-wrens (*Malurus cyaneus*) to playback of acoustically similar scrubwren (*Sericornis frontalis*) aerial alarm calls. First, if call similarity prompts escape independent of learning, then fairy-wrens should flee to playback of scrubwren calls outside their geographical range. However, fairy-wrens fled only in sympatry. Second, if call similarity is necessary for learning heterospecific calls, then fairy-wrens should not respond to sympatric species with different calls. We found, on the contrary, that fairy-wrens fled to the very different aerial alarm calls of a honeyeater (*Phylidonyris novaehollandiae*). Furthermore, response to the honeyeater depended on the specific structure of the call, not acoustic similarity. Overall, call similarity was neither sufficient nor necessary for interspecific recognition, implying learning is essential in the complex task of sifting the acoustic world for cues about danger.

Keywords: alarm calls; signal evolution; predation; communication network; eavesdropping

1. INTRODUCTION

Many species of birds and mammals give alarm calls to warn conspecifics about danger (Caro 2005), which creates both an opportunity and problem for other species. The opportunity is that individuals could use alarm calls of other species to provide information about predators. This is potentially invaluable, as heterospecifics can provide more eyes to watch for danger, and complementary ability to detect or provide information about predators (Bshary & Noë 1997; Goodale & Kotagama 2005). However, the problem is how individuals recognize which calls given by other species are alarm calls, as responding to false alarms would reduce other activities such as foraging. Two contrasting hypotheses about alarm call recognition are that individuals learn which calls are alarm calls (Griffin 2004) or that alarm calls are recognized because they share acoustic properties with those of conspecifics (Marler 1957).

There is evidence of learning about heterospecific alarm calls in some mammals, but minimal evidence among birds (Griffin 2004). For example, golden-mantled ground squirrels, *Spermophilus lateralis*, respond to yellow-bellied marmot, *Marmota flaviventris*, alarm calls (Shriner 1998), and can learn to associate a neutral, novel sound with the appearance of a model predator, suggesting that squirrels can learn to recognize heterospecific alarm calls (Shriner 1999). Similarly, young vervet monkeys, *Cercopithecus aethiops*, acquire the ability to respond to the alarm calls of starlings as they age, and do so more quickly when exposed to more starling alarms, suggesting learning

(Hauser 1988). Learning rather than similarity is likely to be important in species responding to heterospecific alarm calls that differ from their own, such as among birds (Hurd 1996; Templeton & Greene 2007), among mammals (Shriner 1998; Zuberbühler 2000; Fichtel 2004) and when birds respond to mammal alarms (Rainey *et al.* 2004) or mammals respond to bird alarms (Müller & Manser 2008).

Little is known about whether acoustic similarity affects call recognition of heterospecific alarm calls. Among birds, swamp and song sparrows (*Melospiza* spp.) respond to each other's distress calls, which are similar in structure, but not to those of white-throated sparrows (*Zonotrichia*), which are different (Stefanski & Falls 1972), and apostle birds, *Struthidea cinerea*, respond to the unfamiliar but acoustically similar mobbing calls of the Carolina wren, *Thryothorus ludovicianus* (Johnson *et al.* 2003). Similarly, some bats respond to distress calls of unfamiliar species apparently owing to acoustic similarity (Russ *et al.* 2004).

The alarm calls given by passerines to hawks provide a textbook example of signal design (Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003), and an opportunity to assess the significance of acoustic similarity compared with learning in recognition of heterospecific calls. Marler (1955) showed that 'seeet' aerial alarm calls of many European birds, frequently given to hawks, were similar in structure among species. Their high pitch (approx. 6–9 kHz) and narrow bandwidth make these calls difficult for hawks to hear and locate (Klump 2000), so that selection imposed by hawks may have resulted in call convergence, which then permits recognition among species (Marler 1957). The suggestion is plausible because some species do respond to playback of aerial alarms of other species (Magrath *et al.* 2007), and

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animals often generalize responses from familiar to unfamiliar stimuli that are similar (Ghirlanda & Enquist 2003). Furthermore, alarm signals vary among and within individuals (Blumstein & Munos 2005; Leavesley & Magrath 2005; Templeton et al. 2005), and are affected by the environment as they propagate (Wiley & Richards 1982), so selection might favour broad generalization from 'typical' conspecific calls, which could encompass even moderately similar calls of other species. Assessing the consequence of call similarity specifically of aerial alarm calls is important because these calls are both structurally and functionally different from mobbing calls. While aerial alarm calls are cryptic and prompt escape from transient threats, mobbing calls are conspicuous and incite others to approach and harass a stationary predator (Klump & Shalter 1984). There could therefore be less opportunity to learn to recognize the aerial alarm calls of other species, so that structural similarity might be relatively more important.

Understanding the mechanism of heterospecific recognition gives insight into signal evolution and is relevant to conservation. If similarity in call structure affects heterospecific response, call convergence among species may be a consequence of interspecific communication, and not merely the unselected outcome of adaptation to thwart predator eavesdropping. If individuals benefit from warning heterospecifics of danger and more similar calls are better understood, then they may evolve calls more similar to those species. Warning individuals of other species could bring immediate selfish benefits such as inciting others to flee at the same time and so reduce personal exposure (Sherman 1985), or longer term benefits of grouping with other species (Ridley et al. 2007). Interspecific communication could therefore affect signal evolution, as it is known to do in other contexts, such as brood parasitism (Sorenson et al. 2003). Alternatively, if individuals learn to recognize heterospecific alarm calls, there may be no such selection on call structure. Learning and call similarity might nonetheless interact if individuals learn heterospecific calls more quickly if they are more similar to their own—analogous to the way passerines have biases in learning conspecific calls or songs (Davies et al. 2004; Hultsch & Todt 2004). In addition to insight into signal evolution, understanding mechanisms of recognition is critical in conservation practices such as captive breeding and translocation (Griffin et al. 2000).

In this paper, we test whether the response by superb fairy-wrens (*Malurus cyaneus*) to white-browed scrubwren (*Sericornis frontalis*) aerial alarm calls depends on call similarity. These species have similar, high-pitched calls and flee to playback of each other's aerial alarm calls (Magrath et al. 2007). We played back scrubwren calls to fairy-wrens where the species occur together (sympatry) and where fairy-wrens occur alone (allopatry), to test whether recognition depends on familiarity rather than similarity, and played back the calls of another species with a quite different aerial alarm call, to test whether the recognition requires similarity, learning or both.
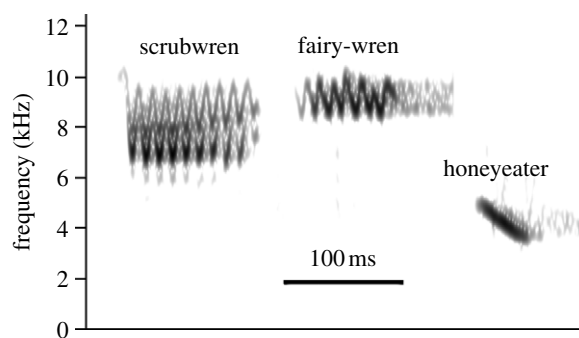

Figure 1. Spectrograms of superb fairy-wren, white-browed scrubwren and New Holland honeyeater aerial alarm calls recorded in Canberra. Spectrograms were prepared in CANARY v. 1.2.4, with settings as described in the text for call analysis, with harmonics excluded; each example has measures similar to the mean for that species.

149°06′ E), Australia, where all three species are common residents. Sites included the Australian National Botanic Gardens and parks around Lake Burley Griffin (Magrath et al. 2007). We also studied superb fairy-wrens in August 2006 and December 2007 in the Macquarie Marshes Nature Reserve (30°40′ S 147°30′ E), 650 km north of Canberra, on the western edge of their range but outside the range of scrubwrens (Barrett et al. 2003). Both locations have resident populations of raptors and large avian omnivores, which prompt aerial alarm calls from all three species (Leavesley & Magrath 2005; R. D. Magrath et al., 2006–2007 personal observations). Raptors include the collared sparrowhawk, *Accipiter cirrocephalus*, which preys on small birds (Marchant & Higgins 1993). The pied currawong, *Strepera graculina*, is an omnivorous predator of fairy-wrens and scrubwrens in Canberra, but does not occur in the Marshes. The Botanic Garden fairy-wrens and scrubwrens were individually colour-banded, otherwise groups were identified by spatial separation.

Fairy-wrens (9–10 g; Maluridae) and scrubwrens (12–14 g; Acanthizidae) are small cooperatively breeding passerines (Higgins et al. 2001; Magrath 2001). These insectivorous species feed primarily on the ground, defend territories during the breeding season and can occur together in mixed-species flocks in the non-breeding season (Bell 1980; Higgins & Peter 2002; R. D. Magrath et al., 2006–2007 personal observations). New Holland honeyeaters (Meliphagidae) are larger (approx. 19 g), pair-breeding residents (Frith 1976). They feed in vegetation on nectar and arthropods (Higgins et al. 2001). Fairy-wrens have high-pitched aerial alarm calls that overlap completely in frequency with scrubwren aerial alarm calls (figure 1; Magrath et al. 2007). They have the same high frequency and duration, and both are rapidly frequency modulated about a constant carrier frequency, but they are distinguishable because fairy-wren calls have a higher peak frequency (9.1 versus 7.1 kHz) and a narrower frequency range (2.3 versus 4.3 kHz; Magrath et al. 2007). By contrast, New Holland honeyeaters have calls that decline smoothly in frequency from approximately 5 to 3 kHz, so they have a different structure and do not overlap in frequency with fairy-wren calls (Jurisevic & Sanderson 1994; §3).

2. MATERIAL AND METHODS

(a) *Study site and species*

We studied superb fairy-wrens, white-browed scrubwrens and New Holland honeyeaters, *Phylidonyris novaehollandiae*, from March 2006 to November 2007 in Canberra (36°16′ S,

(b) *Recording and call analysis*

Methods of recording and acoustic analysis follow Magrath et al. (2007). In brief, we prompted aerial alarm calls using a gliding model sparrowhawk, and recorded calls from a distance of 4–7 m with a Sennheiser ME66 or ME67

directional microphone onto a Marantz PMD670 digital recorder, sampling wave files at 44.1 kHz. In some cases, a currawong model was used in Canberra, but the type of model did not affect call structure (Magrath *et al.* 2007). We calibrated recordings in CANARY v. 1.2.4 using a sound file of known amplitude, and analysed spectrograms in CANARY v. 1.2.4 using a temporal grid resolution of 0.1814 ms with a 96.88 per cent overlap, a frequency grid resolution of 43.07 Hz with an FFT size of 1024 points, a Blackman window function and smooth display style. We set the screen display to 5 ms cm^{-1} and 0.8 kHz cm^{-1}, and for each call element measured: (i) duration (ms), (ii) average amplitude (dB re 1 pWm^{-2}), (iii) lowest frequency (kHz), (iv) highest frequency (kHz), (v) frequency range (kHz), and (vi) peak frequency (frequency at maximum amplitude, kHz). For the fairy-wren, we also measured (vii) the rate of frequency modulation (Hz), excluding partial cycles at the beginning or end of the element. In each case, we selected a high-quality element for analysis, with the best signal-to-noise ratio. If two or more elements had the same quality, we used a random number generator to select among them. Measurements excluded harmonics that, if visible at all, were over 20 dB lower in amplitude than fundamentals.

(c) *Playback experiments*

We carried out two playback experiments. In experiment 1, we broadcast scrubwren alarm calls to fairy-wrens at both sympatric (Canberra) and allopatric (Macquarie Marshes) sites. If call similarity allows fairy-wrens to recognize scrubwren alarms, then fairy-wrens should respond to playbacks at both sites, whereas they should respond only in sympatry if learning is necessary. At each site, we broadcast four-element scrubwren alarms, four-element fairy-wren alarms and three neutral controls to 15 groups of fairy-wrens, a repeated-measures design that followed methods in Magrath *et al.* (2007). Fairy-wren alarms were a positive control, and the neutral controls were background sounds recorded at the same time as the two alarm calls and contact calls of galahs, *Cacatua roseicapilla*, harmless cockatoos that are common at both sites. Each playback contained a single call, and all five playbacks to all 15 groups at a site were unique, so there was complete replication. The same set of playbacks was used at each site. Alarm calls and galah control sounds were broadcast at a natural level of 61 dB at 6 m (midway between mean and maximum recorded for fairy-wrens and scrubwrens), with background sound amplified by the same factor as alarm calls on the same recording. Playbacks were carried out in random order when the focal (closest) bird was at least 0.5 m from cover and approximately 8 m from the observer, who then scored the bird's response as: (0) none; (1) scan (stop and look ≥1 s); (2) flee but land out of cover; or (3) flee to cover. In Canberra, where birds were accustomed to people, playbacks were to birds feeding on the ground, while, in Macquarie Marshes, we also broadcast to birds perched a sufficient distance from cover, because the birds were less likely to feed on the ground near people. Playback sounds were broadcast using a Sony CD Walkman D-EJ751 connected via an amplifier to a response dome speaker (1.5–20 kHz), with equipment mounted around the observer's waist.

Experiment 2 tested whether fairy-wrens could learn to recognize only those heterospecific calls that were similar to their own, by playing back the very different New Holland honeyeater aerial alarm calls to fairy-wrens in Canberra. We broadcast natural honeyeater alarm calls (in which elements have a descending frequency), computer-reversed alarm calls (elements ascending in frequency) and crimson rosella calls (*Platycercus elegans*, neutral parrot control), all at the mean natural amplitude of honeyeater alarms of 70 dB at 6 m. Similar to the construction of fairy-wren and scrubwren alarms, we composed honeyeater alarm calls by pasting single elements at mean natural intervals (64 ms), standardized to eight-element calls (within the natural range recorded for 1–44 elements). Computer-reversed calls were designed to test if the response was specific to New Holland honeyeater alarms, which implies learning, or to more general acoustic features, such as element peak frequency or rapid repetition, which were not affected by reversal and may not require learning. Playback protocol and equipment were the same as in experiment 1, except that each playback was to a different group, rather than using a matched design, so there was a total of 45 groups. Response scoring was the same as in experiment 1, except we also scored if birds scanned before fleeing to cover, a response not seen in the previous experiment.

(d) *Statistical analyses*

We used *t*-tests to compare acoustic characteristics of calls. Responses to playback were categorized for most analyses as 'flee immediately to cover' or 'not flee immediately to cover'. Variability among those not fleeing was analysed if present. Analysis of experiment 1 used Cochran's *Q*-tests for a change in the proportion of responses according to repeated-measures playbacks within a group (Sokal & Rohlf 1995). The comparable McNemar test was used when contrasting two treatments. Experiment 2 was based on independent samples, and so we used chi-squared and Fisher's exact probability tests to test for an association between playback type and response. All tests were two-tailed and carried out in SPSS v. 13.0 for Macintosh (SPSS Inc., Chicago, IL).

3. RESULTS

(a) *Call structure*

We found no difference in aerial alarm call structure between Canberra and Marsh fairy-wrens (Canberra ($n=15$) versus Marsh ($n=21$): duration (ms) 104.3 ± 31.5 versus 126.2 ± 44.2, $t_{34}=1.64$, $p=0.11$; low frequency (kHz) 8.23 ± 0.29 versus 8.19 ± 0.33, $t_{34}=0.37$, $p=0.71$; high frequency (kHz) 10.61 ± 0.40 versus 10.51 ± 0.34, $t_{34}=0.81$, $p=0.42$; peak frequency (kHz) 9.11 ± 0.37 versus 9.17 ± 0.38, $t_{34}=0.50$, $p=0.62$; frequency range (kHz) 2.38 ± 0.36 versus 2.32 ± 0.40, $t_{34}=0.47$, $p=0.64$; frequency modulation (Hz) 96.3 ± 9.6 versus 102.5 ± 12.0, $t_{34}=1.67$, $p=0.10$; discriminant function analysis, $\chi^2=6.5$, d.f.$=5$, $p=0.26$). The lack of difference means that response to scrubwren playback at the two locations was not confounded by differences in call similarity.

New Holland honeyeater aerial alarm calls were quite different from fairy-wren calls in frequency, duration and call structure. Honeyeater calls had a much lower peak (4.0 ± 0.23 kHz; mean$\pm$s.d.), high (5.2 ± 0.15 kHz) and low (3.1 ± 0.20 kHz) frequencies. They were also shorter (47.9 ± 6.2 ms) and had a descending tone rather than rapid frequency modulation (figure 1). In these measures, there was no overlap between species ($n=15$ for each species in Canberra; *t*-tests, all $p<0.001$). Honeyeater calls were usually louder than fairy-wren calls (70.3 ± 4.1, 63.5–77.6 versus 56.5 ± 4.8, 49.4–65.3 dB; means$\pm$s.d.,
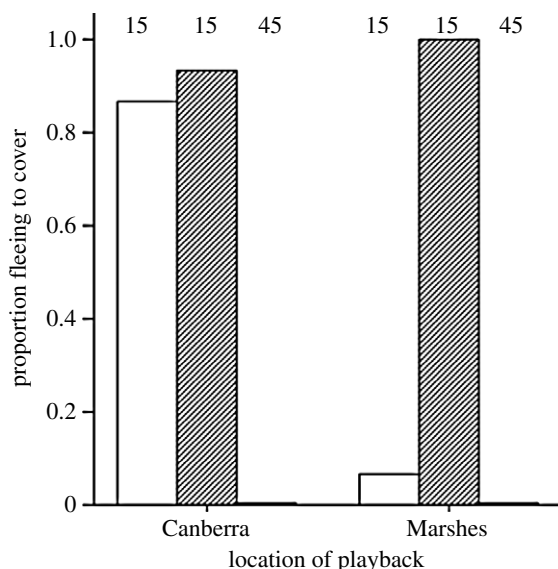
Figure 2. Response of fairy-wrens to playback of aerial alarm calls of conspecifics (hatched bars) and scrubwrens (white bars) in Canberra, where scrubwrens also occur, and Macquarie Marshes, where scrubwrens are absent. There was no response to any of the three controls (black bars, text), so they were combined; the number of playbacks is shown above the bars, and $n = 15$ groups at each site.

range; $t_{28} = 8.5$, $p < 0.001$). The only major overlap was in the frequency range, which nonetheless differed significantly (honeyeater 2.1 ± 0.16, 1.8–2.4 versus fairy-wren 2.4 ± 0.36, 1.7–3.2 kHz; $t_{19.3} = 3.15$, $p = 0.005$, variances not assumed equal).

(b) Experiment 1: playbacks in sympatry and allopatry

Fairy-wrens responded to the aerial alarm calls of scrubwrens only when sympatric, showing that the similarity between their calls did not explain why fairy-wrens responded to scrubwren calls in Canberra (figure 2). In allopatry at the Marshes, fairy-wrens fled to all 15 playbacks of fairy-wren calls but to only 1 out of 15 playbacks of scrubwren calls (NcNemar, exact binomial $p < 0.001$), whereas, in Canberra, fairy-wrens fled equally to each species' alarm (McNemar, exact $p = 1.0$). Birds fled directly to cover or showed no response at all, except for one bird at each location that flew but landed out of cover after a scrubwren playback. Overall, no bird responded to any of the 45 control playbacks at either location, so playback type affected response at each site (Marshes, Cochran's $Q = 56.4$, d.f. $= 4$, $p < 0.001$; Canberra, Cochran's $Q = 52.2$, d.f. $= 4$, $p < 0.001$).

(c) Experiment 2: response to honeyeater calls

All 15 fairy-wrens fled immediately to cover after playback of natural honeyeater calls, but only one did so to playback of the honeyeater call played backwards, and none to the rosella control (figure 3; $\chi^2 = 51.2$, d.f. $= 2$, $p < 0.001$). There was, however, behavioural variability among those 14 birds that did not flee to cover immediately after the backward playback. Six of them showed no response to the playback, six scanned, one scanned and then flew to cover, and one flew immediately but landed out of cover. By contrast, none responded to
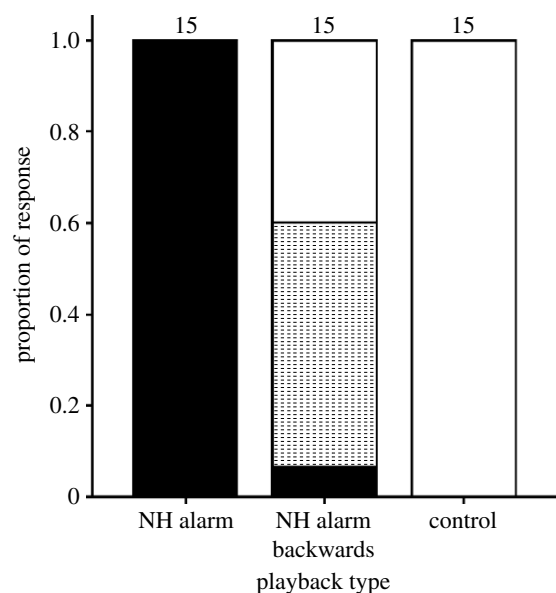

Figure 3. Response of fairy-wrens to playback of New Holland (NH) honeyeater alarm calls played normally (elements descend in frequency) or reversed by computer (elements ascend in frequency) in Canberra, and a neutral control sound (parrot non-alarm call); $n = 15$ individuals for each treatment. Intermediate responses entailed increased vigilance and occasionally also flight (text). Black bar, flee; stippled bar, intermediate; white bar, none.

the rosella playback, so that there was more likely to be at least some response to the backward honeyeater call than to rosella control (9/15 versus 0/15; Fisher's exact probability, two-tailed $p = 0.001$).

4. DISCUSSION

Call similarity was neither sufficient nor necessary to explain fairy-wren recognition of heterospecific aerial alarm calls, whereas learning appears critical and does not depend on call similarity. Despite the similarity of their calls, fairy-wrens fled to scrubwren calls only in sympatry, where they have the opportunity to learn the calls, but not in allopatry, where they do not. Furthermore, fairy-wrens fled to cover to the aerial alarm calls of sympatric New Holland honeyeaters, which have a call of totally different structure, showing that call similarity is not necessary for recognition of other species' calls. All results are consistent with learning, and so imply that birds have the flexibility to take advantage of the warning calls of a wide range of species and so enhance anti-predator defence.

The response of fairy-wrens to scrubwren alarm calls in sympatry but not in allopatry suggests that the birds in sympatry learn to associate scrubwren alarms with danger, rather than responding because they share acoustic characteristics. The two fairy-wren populations had statistically indistinguishable alarm calls, so that the different behavioural response was not due to Canberra fairy-wrens having calls more similar to scrubwrens that do Macquarie Marsh fairy-wrens. Given that these species are vulnerable to similar predators, learning to recognize scrubwren calls is likely to be adaptive. The lack of response in allopatry suggests fine discrimination, given that the species' alarm calls overlap in frequency and both have rapid frequency-modulated calls. Heterospecific calls may therefore need to be very similar to prompt escape

without learning. We know of no species in Canberra with calls more similar to fairy-wrens than those of scrubwrens, but superb fairy-wrens overlap elsewhere with congeners, which might have more similar calls.

Fairy-wrens responded as strongly to New Holland honeyeater alarm calls as to those of scrubwrens and conspecifics despite their completely different call structure, again suggesting learning. New Holland aerial alarm calls had no overlap in frequency with fairy-wren aerial alarm calls, with a much lower peak frequency (4.0 versus 9.1 kHz) and a monotonic decline in frequency rather than rapid frequency modulation. Furthermore, the flight to normal but not to backward versions of honeyeater alarms showed that fairy-wrens responded to the specific structure, rather than the degree of similarity or general properties such as rapid delivery, peak frequency or amplitude. Overall, response to the specific structure of New Holland alarm calls, rather than mean acoustic properties, suggests learning.

The intermediate response to backward honeyeater alarms suggests that call similarity might have a role in promoting learning of heterospecific calls. Although only one fairy-wren fled to playback of backward honeyeater calls, approximately half responded by stopping feeding and scanning, behaviour not shown to control playbacks. One possibility is that acoustic similarity of backward to normal honeyeater calls prompted alertness, which may in turn lead to faster learning of meaning. If this is true, there may be an interaction between learning novel calls and receiver biases or previously learned calls, as has been shown for conspecific song (ten Cate & Rowe 2007). Other possibilities are that the partial response to backward calls reflects call novelty, or that the backward call retains some general property of alarm calls.

Taken together, our experiments suggest that birds learn to recognize aerial alarm calls of other species, and that such learning does not require similarity to conspecific calls, although similarity might increase the speed of learning. We do not know the mechanism of learning, and there appears to be nothing known about learning to recognize heterospecific alarm calls in birds (Griffin 2004). Birds might learn through association of a heterospecific call with predators, as in ground squirrels (Shriner 1999), or through social learning, in which individuals learn to associate heterospecific alarm signals with conspecific signals or other anti-predator behaviour (Curio *et al.* 1978; Mizra & Chivers 2001; Griffin 2004). In birds, response to conspecific alarm calls can occur in nestlings or recent fledglings (Davies *et al.* 2004; Madden *et al.* 2005*a*,*b*; Magrath *et al.* 2006), which may then allow associative learning about heterospecific calls. Although consistent with learning, our results provide only indirect evidence, and it is possible that Canberra fairy-wrens have evolved innate responses to the calls of sympatric species. Our results emphasize the need for direct tests of whether and how birds learn to recognize heterospecific alarm calls.

Learning has the disadvantage of requiring experience but the advantage of plasticity, so that a species can potentially use a diversity of alarm calls given by the local bird community (Griffin 2004). This diversity can even extend to learning to recognize the alarm calls of mammals (§1). The very specific responses by fairy-wrens to heterospecific aerial alarm calls, and similar findings in

other species on mobbing alarms (Rainey *et al.* 2004; Templeton & Greene 2007), suggest that learning might be crucial in allowing use of other species' calls but also avoiding false alarm responses to benign calls. Simply generalizing from conspecific alarm call structure may risk false alarms to heterospecific calls of similar structure but different meaning. Scrubwrens, for example, have several high-pitched calls in their repertoire, including contact calls, so that fairy-wren flight to all high-pitched calls would be unnecessary and costly. Learning is therefore likely to help birds in the extraordinarily complex task of sifting the acoustic world for cues about danger.

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